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Is male care compromised by additional mating opportunity?

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In many animals, males contribute substantially to caring for their young but also have the opportunity to enhance their reproductive success by attracting additional mates or by seeking copulations with females that are already paired to other males. Sometimes, the opportunity to gain these additional matings coincides with periods when males are providing parental care. At such times, males might be expected to allocate time and effort to these alternative behaviours in a way that maximizes their overall reproductive success. But do they? Here, we examine the recent evidence for a tradeoff between parental effort and additional mating effort and highlight some of the factors that might influence how this conflict is resolved. We conclude that, in spite of the paucity of comprehensive studies, this tradeoff has a potentially important and often overlooked influence on parental behaviour in a range of taxa.

The males of many taxa contribute to one or more aspects of parental care, such as the feeding and defence of young [1,2]. In most of these species, males also seek to enhance their reproductive success by mating with more than one female over the course of a single reproductive event. In species that breed in social pairs, such as most birds, this can be achieved by mating with females that are already paired to another male (extra-pair copulations; EPCs) [3]. Alternatively, the males of polygynous species can gain further matings by attracting additional social partners [4]. Even among species where males provide sole care of the offspring and do not pair socially, they might have the opportunity to gain multiple matings by allowing several females to leave them eggs [1].

Sometimes, the opportunity to gain additional matings might coincide with periods when males are already providing parental care, and so males will be confronted with the dilemma of how best to allocate time and energy (effort) to these alternative behaviours [3,5]. This predicted tradeoff between parental effort (PE) and additional mating effort (ME) has attracted much interest, especially over the past decade, following the discovery that extra-pair fertilizations (EPFs) are an important component of male reproductive success in many birds [6]. But in spite of this recent interest, little effort has been made to review critically the accumulating evidence for this potentially important determinant of parental behaviour. Here, we aim to redress this situation by examining some of the most recent empirical studies and assessing the progress that has been made in revealing and understanding the tradeoff between these potentially conflicting forms of male reproductive behaviour.

We focus specifically on scenarios in which males have the opportunity to invest simultaneously in PE and ME, as part of a mixed reproductive strategy [7]. In some biparental species, including a range of fish, birds and some insects, one parent sometimes deserts the current brood to seek a subsequent mate, leaving the other parent to care for the brood alone [8]. For example, males of the biparental cichlid fish *Herotilapia multispinosa* are more likely to abandon their current brood as the sex ratio of adult females in the population increases because they have an improved chance of subsequently re-pairing [9]. This decision to desert represents one solution to the tradeoff between PE and ME [8], but here we focus on scenarios in which both PE and ME occur concurrently rather than sequentially.

The tradeoff between PE and ME might also be resolved over evolutionary time such that responses become fixed rather than facultative [5,10,11]. For example, frequent opportunity for EPCs or attracting extra social mates might explain why the males of some birds have either never evolved incubation behaviour, or have lost the disposition to incubate. Such fixed solutions could account for some of the interspecific variation in male parental behaviour [12]. However, here, we focus on the variation in reproductive behaviour observed within and between populations, drawing our examples primarily from birds, but also from a range of other taxa that exhibit paternal care.

PE and ME might not always be incompatible. Particularly in species with male-only care, including some fish and arthropods, parental care can also attract mates [13]. For example, male harvestmen spiders *Zygopachylus* construct elaborate mud nests in which several females can lay their clutches. When given the choice, female *Z. albomarginis* favour mating and leaving eggs with males that are already guarding clutches [14]. Here, however, we discuss the more common situation in which acquiring additional matings is likely to conflict with performing parental duties, even though delineation between the two activities is not always clearcut.

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Box 1. Defining the tradeoff between parental care and additional mating effort

A common approach to modelling the reproductive behaviour of individuals is to divide their reproductive effort into three distinct components: parental effort (PE; actions to increase offspring fitness), mating effort (ME; actions to gain matings with females additional to the initial mate) and somatic effort (SE; actions to increase survival) [5,10,58] (Fig. I). As each individual has only a fixed amount of effort to expend, an increase in effort for one component must be accompanied by a decrease in the allocation of effort to one or both of the others. This model is illustrated in Fig. I, where we see that an increase in PE from resolution one (R^1) could result in anything from a decline (R^2) to an increase (R^3) in ME, depending on the concurrent change in SE. Consequently, demonstrating a tradeoff between PE and ME requires showing that an observed increase in PE is actually accompanied by a decline in ME or vice versa.

Males should be selected to optimize allocation of effort to these three components in each breeding attempt, so as to maximize their lifetime reproductive success. Optimal allocation will depend on the relative fitness returns for each component. Any factor that changes the fitness return for one component will have a direct effect on one or both of the other two. For example, if fertile females are plentiful in the population, the net benefit of ME compared with PE might be high, and males might allocate more time to the pursuit of additional matings at the expense of PE and/or SE. By contrast, if there are very few fertile females, the returns from ME might be minimal compared with those from PE and/or SE, and so males should forgo seeking additional mates.

Optimal investment in reproductive effort will also depend on the shape of the functions linking each component to fitness [5,59]. For example, Fig. II shows two alternative hypothetical functions linking male PE to fitness (f^1 = curvilinear with diminishing returns, and f^2 = sigmoidal) plotted against a fixed linear fitness return from the sum of ME + SE. Note that the optimal tradeoff resolutions (dashed vertical lines R^1 and R^2) are markedly different depending on which of these two functions applies. Thus, accurate prediction of tradeoff resolution requires information not only about the potential benefits of each component, but also about the shape of the relationship between each component and fitness.

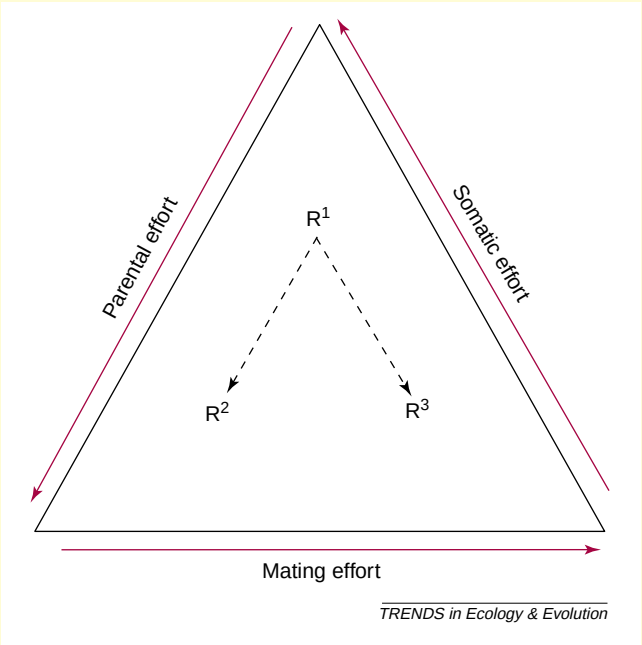

Fig. I.

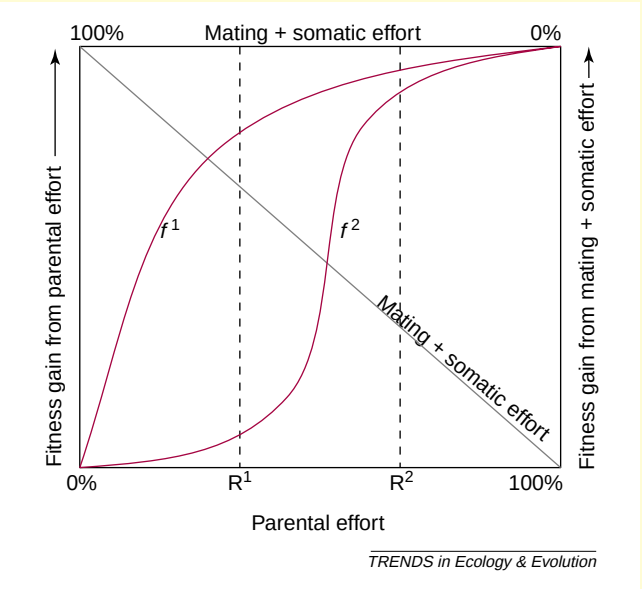

Fig. II.

Factors influencing resolution of the tradeoff

The tradeoff between PE and additional ME can be defined in terms of a simple model of male reproductive behaviour (Box 1). Essentially, a tradeoff requires demonstrating a causal and inverse correlation between PE and ME. Generally, positive relationships between both PE and ME with male fitness would also be anticipated, otherwise a tradeoff would be unnecessary.

The optimal resolution of a tradeoff should depend on those variables that influence the profitability of either PE or ME. Reproductive returns from these behaviours can vary in relation to particular characteristics of a male (or his partner), such as age or quality [6,11,15]. Additionally, a range of ecological factors, common to all males in the population, can influence the fitness returns from PE or ME [3]. Thus, optimal allocation of reproductive effort should depend on the interaction between the particular phenotype of a male and his environment [16]. A common approach to investigating this trade off has been to use natural variation in PE or ME, or experimental manipulation of factors that are expected to influence the value of PE or ME, and then determine whether the predicted shift in effort is observed. Below, we highlight a range of factors that are likely to influence these two components of reproductive behaviour, and discuss some recent studies that consider these variables. These and other factors are summarized in Table 1.

Another popular and fruitful approach to investigating the conflict between PE and ME has been to examine the proximate mechanisms of control [17]. Among birds, several hormones have been implicated in mediation of this tradeoff and we outline these mechanisms in Box 2 with reference to some recent studies.

Effect of phenotype on tradeoff resolution

The success of males at gaining additional matings usually varies with phenotype. Among birds, for example, male EPF success has been shown to co-vary with several traits,

Table 1. Summary of factors predicted to influence resolution of the tradeoff between parental and addition mating behaviours[a]

Factor type	Factor	Predicted change in PE and/or ME	Refs[b]
Male phenotype	Secondary sexual trait	Increase in ME by males with greater trait expression	[22,24,26]
	Age	Increase in ME with age (but could also be concurrent increase in benefits of PE)	[21,22]
	Testosterone level	Increase in ME and decrease in PE with elevated testosterone	See Box 2
Benefit of ME	Proportion of fertile females	Increase in ME with greater proportion of fertile females	[20,21,24,35]
	Population sex ratio	Increase in ME with greater proportion of females	[9]
	Population density	Increase in ME with greater population density	[6,12,37,38]
	Nest site availability	Increase in ME with availability of nest/spawning locations	[40,42]
	Time of day	Increase in ME at time when copulation attempts most successful	[35]
Benefit of PE	Clutch/brood size	Increase in PE with increase in clutch/brood size	[21,42,43]
	Number of helpers	Decline in PE with increase in social group size	[46–49]
	Confidence of paternity	Decline in PE with reduced certainty of paternity	[5,10,11,44,45]
	Food availability	Decline in PE with increase food availability	[50–52]
	Temperature	Decline (avian incubation) or increase (egg care in fish) in PE with temperature	[57]
	Nest predators	Increase in PE with greater risk of clutch/brood predation	[53]

[a]Abbreviations: ME, mating effort; PE, parental effort.
[b]Cited references relate to predictions, but are by no means an exhaustive list of all relevant studies.

including plumage ornamentation, body size, song repertoire and body condition [6,15]. Older males are also often more successful at gaining EPFs than are their younger counterparts [18,19]. The association between these traits and EPF success might arise because older or high-quality individuals invest more in ME and/or are preferred by females as extra-pair mates. Quantifying ME is notoriously difficult because extra-pair displays are often inconspicuous and usually occur away from the nest site [20]. However, available data suggest that ME varies widely among males in many populations [20–23], and sometimes correlates with variation in phenotypic traits [21,22]. For example, only those male superb fairy-wrens *Malurus cyaneus* in nuptial plumage engage in extra-pair displays and gain EPFs [22,24]. Thus, high-quality males might be expected to invest more in ME at the expense of PE, resulting in a negative correlation between the two. However, a high level of ME might not necessarily translate to a low level of PE, as high-quality males might be able to invest relatively more in both activities because they can afford to invest less in somatic effort (SE; Box 1). Consequently, correlations across individuals might fail to reveal negative relationships between PE and ME because these behaviours are positively correlated within phenotype [25].

To avoid this complication, several recent studies have quantified male PE after manipulating traits associated with attractiveness, presumably altering the success of a male of gaining additional mates or copulations, without changing his parental ability. For example, male bluethroats *Luscinia svecica* with experimentally reduced ornamental throat patches advertised less for additional mates and tended to gain fewer EPFs than did control males, but did increase nestling provisioning [26]. Conversely, experimental enhancement of attractiveness in collared flycatchers *Ficedula albicollis* led to reduced nestling feeding rates, apparently because of greater competition with other males [27]. Interestingly, this negative relation between male attractiveness and level of paternal care is also forecast by the differential allocation hypothesis (DAH) [28], but for different reasons. The DAH predicts that high-quality individuals can reduce PE because their partners tend to invest more to gain the indirect benefit of high-quality offspring. Perhaps the extent to which high-quality males reduce PE relates to the opportunity to gain additional matings, which might help explain the contrasting results of studies investigating male attractiveness in relation to PE [29].

Box 2. Proximate mediation of the PE–ME tradeoff in birds

Several hormones have been implicated in the proximate control of reproductive behaviour in male birds [17]. Parental behaviour is typically associated with high levels of the hormone prolactin [60], whereas elevated levels of the steroid hormone testosterone commonly promote mating behaviours, but also suppress parental activities [17]. For example, male dark eyed juncos *Junco hyemalis* with experimentally enhanced levels of testosterone sing more, expand their home-ranges and gain more extra-pair fertilizations, but they also reduce feeding to nestlings and are less effective at detecting nest predators than are control males [17]. Together with many other studies, these findings suggest that testosterone might directly mediate the parental effort–mating effort (PE–ME) tradeoff. However, the mechanism by which this steroid might interfere with care behaviour remains unclear [61], and its inhibitory effect is not universal to all species. For example, elevated testosterone in male great tits *Parus major* promotes sexual activity but fails to suppress nestling feeding rate [62]. At least in some species, therefore, the effect of testosterone on PE might be indirect and somewhat flexible. Furthermore, the influence of testosterone can vary markedly between individuals. In a recent study of the superb fairy-wren *Malurus cyaneus*, males were shown to maintain high levels of testosterone throughout the breeding season, but still provide substantially for their broods [63]. Nevertheless, experimental elevation of testosterone, within the natural range, resulted in a marked decline in provisioning rate [64]. It seems that male fairy-wrens maintain testosterone at individually optimal levels that do not interfere with parental duties, but which enable them to continue pursing extra-pair copulations, the primary avenue for paternity in this species [64]. So, although testosterone clearly plays a key role in regulating the reproductive behaviour of male birds, a better understanding of the physiological processes will be crucial to a comprehensive understanding of the PE–ME tradeoff.

Hormone manipulation studies also provide an opportunity to evaluate whether males are optimizing the tradeoff between PE and ME, because modified hormone profiles should result in suboptimal allocation of reproductive effort [17]. In the dark-eyed junco, testosterone-treated males had lower annual output from their own nests, but benefited from a reduced level of cuckoldry and an increase in EPF success, compared with control males [65]. Overall, there was no detectable difference in the net annual reproductive success of treated versus control males. This suggests that either there were several equally profitable solutions to the tradeoff or that treated males reduced somatic effort, which would ultimately be reflected in lower survivorship [17,65].

These examples illustrate how the phenotype of a male can influence his investment in PE and ME, but the reverse can also occur. Male collared flycatchers, for example, that were induced to provide more (or less) PE in one season (by brood-size manipulations) returned in the following year with a decrease (or increase) in the size of their white forehead patch [30]. Patch size correlates positively with EPF success in this species and can be considered a form of ME [31]. In this case, current reproductive behaviour in part reflects previous allocation decisions, suggesting that PE and ME, similar to many life-history traits, can be traded-off over an individual's lifetime [32,33].

Factors influencing the value of additional mating effort

Variation in the availability of fertile females. The proportion of sexually receptive females in any population will vary over the course of the breeding season, and this can influence the likelihood of a male gaining additional matings. In populations that breed synchronously, most females will be receptive simultaneously and there will be minimal opportunity for additional mating once parental care commences, and hence little reward for ME. By contrast, in populations that breed asynchronously, a proportion of females will usually be receptive when some males are providing parental care. In this situation, male ME might vary depending on the availability of females that are fertile.

Several studies of territorial bird species have shown that the amount of time males spend off-territory increased with the number of neighbouring females that were fertile, although no concurrent reduction was observed in male provisioning [20,21,24,34]. However, in these studies, the number of fertile neighbours was typically low during the period when males were feeding nestlings, so, at best, only a weak correlation might be anticipated.

In species that nest in aggregations, the opportunity for males to interact with fertile females should be greater than in territorial species. In the colonial nesting fairy martin *Cecropis ariel*, the contribution to incubation by individual males declined with the proportion of fertile females present in the colony [35]. Furthermore, the incubation period of the clutch was longer at nests where males contributed less to incubation, suggesting a cost to reduced male PE. These data are consistent with a shift from PE to ME, although the key question of whether reduced PE translated to an increase in ME was not addressed.

The opportunity for additional matings can also vary diurnally. In most birds, the frequency of copulation varies over the course of the day [36], so males might be expected to concentrate ME to periods of the day when such activities are likely to be most successful. Consistent with this prediction, the negative correlation between male incubation attendance and availability of fertile females in the fairy martin was most pronounced in early–mid morning, when copulations were most frequently observed [35].

In most populations, the probability of males encountering fertile females will also increase with population density, and several lines of empirical evidence indicate that there can be a corresponding increase in the frequency of EPFs [6,37,38]. Consequently, a shift from PE to ME might be predicted as population density increases. However, we are unaware of any studies that report on male ME or PE in relation to population density, although a recent comparative study has linked avian families with male-only care to low population density and vice versa [12].

The availability of females has even been suggested to influence the level of male care in humans. The Hadza are hunter-gathers of northern Tanzania who live in camps of variable population size and sex ratio. In a study of six camps ranging in size from 12–108 inhabitants, several measures of male care were found to decline with both the absolute number of women of fertile age and the ratio of females to males in camp [39]. This correlation might indicate a shift in male effort from PE to ME, although other demographic or social factors associated with camp size and/or sex ratio might confound this correlation. Furthermore, similar to the fairy martin study, it was unclear whether the time saved on PE was allocated to ME.

Variation in availability of nest sites. In facultatively polygynous species, the availability of potential nest or spawning sites might influence male ME, because an abundance of sites could increase the likelihood of polygyny. This hypothesis has been experimentally tested in European starlings *Sturnus vulgaris,* by providing empty nest boxes adjacent to the boxes already occupied by socially monogamous pairs [40]. This resulted in males decreasing their contribution to incubation, spending more time singing, and increased their probability of obtaining an additional mate. Singing is involved in mate attraction in starlings [41], and the shift from PE to ME appears to result from the change in likelihood of securing an additional mate.

Factors influencing the value of paternal care

Size of the clutch or brood. Westneat [21] suggested that the optimal tradeoff resolution should vary with the size of the clutch or brood of a male. Males with larger clutches or broods might invest more in PE at the expense of ME, because the relative value of PE should be greater. This was tested in the polygamous scissor-tailed sergeant *Abudefduf sexfasciatus*, a tropical damselfish in which care is provided solely by the male. Typically, males court and mate with several females over a few days before commencing 4–5 days of full-time egg care. Reduction of the total egg number during the first day of the parental phase, however, resulted in males providing less care than did control males, and temporarily reverting to courtship activities in an effort to induce spawning by additional females [42].

A similar shift in allocation has also been observed in the European starling. Male contribution to incubation, relative to that of the female, increased for experimentally enlarged clutches and vice versa [43]. Furthermore, males with reduced clutches spent more time singing and carrying green plant material to adjacent nest boxes (presumed courtship behaviours), and were more likely to gain a secondary female.

Are changes in male contribution to PE also observed in

relation to brood size? An overview of experimental studies reveals no consistent pattern; several show the predicted increase, others reveal no change, and some report a decline [43]. However, a positive relationship between the share of provisioning by the male and brood size would only be expected if there were concurrent opportunities for additional matings. Perhaps the differences between studies can be explained, in part, by variation in additional mating opportunity.

The value of the brood to a male might also change in relation to his perceived level of paternity [10]. Several studies have identified cues that males apparently use to assess paternity and subsequently adjust their level of PE [5,11,44,45]. Males that reduced PE in response to lower confidence of paternity must be diverting effort into ME and/or SE, although none of these studies has examined the effect of reduced paternity certainty on ME. Indeed, variation in additional mating opportunity might also account for some of the contrasting findings among the many studies of male response to reduced paternity.

Social context. In animals that breed in social groups, the importance of male care might depend on the number, age or sex of other group members. Auxiliary carers might largely compensate for reduced PE by the genetic father, enabling him to invest more in seeking additional matings. This occurs in the cooperatively breeding superb fairy-wren, where dominant males with helpers typically feed nestlings at a lower rate [46,47], spend more time displaying to extra-group females, and tend to enjoy greater EPF success [48]. Furthermore, these males have no higher survivorship between seasons than do males without helpers, suggesting that the benefits of reduced PE are directed to ME rather than SE. However, the association shown between PE and ME in this study was correlational and could reflect phenotypic differences among males. Furthermore, dominant males with helpers typically suffer a higher level of cuckoldry than do those without [48], so the observed reduction in PE might reflect their lower confidence of paternity in addition to the reduced importance of PE by the dominant (but see [49]).

Food availability. Food availability usually varies in both time and space. When food is abundant, the relative energetic cost to parents of offspring care should decline [50]. Under such conditions, males might allocate more to ME, because less effort is required to provision the brood, or their partner is more easily able to compensate for shortfalls in male care. Consistent with this idea, the contribution to nestling feeding (relative to their mate) by male serins *Serinus serinus* declined as food abundance increased [51], although there was no evidence that these males were spending more time pursuing EPCs.

Food availability, however, does appear to influence male effort to attract additional mates in some biparental burying beetles *Nicrophorus* spp. [52]. Pairs defend and prepare small vertebrate carcasses that serve as the food source for their developing young. If a carcass is large enough to support more than the brood of one female, males continue to emit sex pheromones so as to attract additional females. The resident female attempts to interfere with this behaviour, presumably to reduce the likelihood of her larvae encountering competition [52], although it is unclear whether male care is compromised by his efforts to recruit additional females.

Predation pressure. In some taxa, males guard their eggs and/or young from predators. Here, the risk of predation might influence the relative value of PE and ME, assuming that ME is largely incompatible with clutch/brood guarding. Predation pressure can vary within or between breeding seasons or between populations. For example, the Seychelles fody *Foudia sechellarum* occurs on two of the three islands occupied by the Seychelles warbler *Acrocephalus sechellensis* [53]. Fodies prey on warbler eggs, but attendance at the nest by male warblers is an effective deterrent against nest predation [53]. On the two islands with fodies, male warblers were shown to attend their nest almost continuously in the absence of the incubating female. However, on the island without fodies, male warblers spent much less time nest guarding and were in better body condition, suggesting a shift from PE to SE. EPFs are common in this warbler [54], and it would be interesting to see if reduced need for nest guarding also translates to greater ME and higher frequencies of EPF.

Prospects

Numerous recent studies, especially of birds, reveal patterns that are consistent with a tradeoff between PE and ME, although few provide conclusive evidence. Typically, studies report the predicted change in PE or ME but not both. Nevertheless, the cumulative evidence from these studies provides a strong case that male reproductive behaviour is sometimes a compromise between these two components of reproductive effort. Factors influencing the likelihood of additional mating success, such as individual phenotype or availability of additional mates, might therefore be an important source of variation in male parental behaviour at the individual, population and interspecific level. Most studies of parental behaviour, however, have tended to ignore these factors. Importantly, variation in mating opportunity could explain some of the inconsistent patterns observed across studies on the effect of paternity, mate attractiveness, and brood size on paternal care.

Among birds, tradeoffs between PE and ME have more commonly been observed during the incubation rather than the nestling feeding period. This might be because incubation precedes nestling feeding and, if the population breeds even a little synchronously, males will generally have greater opportunities for attracting additional mates or gaining EPCs during the incubation period. Furthermore, the tradeoff might be more obvious during incubation because brooding birds are usually confined to the nest for extended periods whereas chick feeding involves regular trips away from the nest, which might enable greater interaction with fertile neighbours. Tradeoffs might also be more evident in colonial than territorial species, because encounters between different individuals in populations of the former are more frequent.

Numerous studies have demonstrated that reduced male care can adversely affect reproductive success [55,56], which is a general assumption of this tradeoff. However, there is much less information available about the relationship between ME and consequent reproductive

success. In most birds, females appear to control copulation access [15], so the relationship between male ME and success might depend on the degree and nature of female choosiness. Clearly, further studies relating ME to mating success would be valuable, particularly where concurrent data are collected on the extent and value of male PE.

Experimental studies have provided the most valuable insights into the PE–ME tradeoff. Some of the predicted influences on tradeoff resolution that we outline here have been examined experimentally (e.g. phenotype, nest site availability and clutch-size), but most have not (e.g. breeding synchrony, population density and sex ratio, food availability, number of helpers and predation pressure). Some of these factors are amenable to manipulation and would provide valuable empirical tests. The most promising taxa to use for such experiments are those where the fitness returns from male PE and ME are reported to vary widely, which includes many birds and some fish and invertebrates. These systems offer exciting opportunities with which to study the complexities and proximate mechanisms of tradeoff resolution.

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